

PROCEEDINGS
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ON TWO ILLINOIS SPECIMENS OF *DIPLOCARDIA*
SINGULARIS, WITH DISCUSSION OF THEIR MODE OF
REPRODUCTION (ANNELIDA; OLIGOCHAETA)¹

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Two undissected, unidentified worms, perhaps also others like it, may have considerably puzzled Frank Smith, the first native-born American to concern himself with oligochaete systematics. The evidence is provided by Smith's failure to identify the specimens, secured by himself in 1901, though he continued to publish on megadriles until 1928. One specimen now is referable to *Diplocardia singularis* (Ude, 1893). Association therewith of the other in a single numbered lot suggests that Smith may have suspected there was some special but hitherto unexplained relationship between the two. That relationship is elucidated below.

Characters of major systematic importance are mentioned in the following brief description to show similarities as well as differences of the two individuals.

Diplocardia singularis (Ude, 1893)

1893. *Geodrilus singularis*, Ude, Zeitschr. Wiss. Zool. 57, p. 69.
(Type-locality, Danville, Illinois. Types, in the Hamburg Mus.?)

1958. *Diplocardia egglestoni* Murchie, Ohio Jour. Sci. 58, p. 270.
(Type-locality, Section 12, Dexter Township, Washtenaw County, Michigan. Syntypes in the U. S. Natl. Mus.)

Illinois

Urbana, woods, 30 April 1901, 0-0-2. F. Smith. (U. S. Natl. Mus. No. 25653. Referred to herein as A and B.)

External characteristics. Size, 110 by nearly 2 mm (A), 75 by 2 mm (B). Segments, 112 (A), 79 (B). Prostomium, epilobous, tongue long

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and open (2 specimens). An equatorial circle of very small spots on each of segments ii-xii, obvious after cuticle floated away, produced an appearance of a ring of setal tips. First dorsal pore, at 8/9 but porelike markings at 6/7, 7/8 (2). Clitellum, annular (2), but lacking ventrally in front of eq/xiii and behind eq/xvii (A), or only in xviii (B), xiii-xviii/2 (A), xiii-xviii (B).

Seminal grooves, wide and shallow (A), lacking (B) or perhaps represented by slight furrows in setal annulus of xix, slightly lateral to A (preservation artefacts?). Male pores, each on slight tubercle in seminal groove, about midway between levels of 18/19 and of presetal secondary furrow in xviii (A), unrecognizable, probably lacking (B). Prostatic pores and apertures of associated setal follicles, unrecognizable, but penial setae of xvii protrude to the exterior conspicuously (A). Prostatic pores, lacking. Ventral setae of xviii-xx, externally recognizable, some of them seemingly of about same size as in adjacent segments, AB about as wide as in adjacent segments, on each side of xx apertures of *a,b* follicles within a transversely elliptical tumescence (B). Genital markings, paired, in AB, postsetal in xvii and xx, each with translucent central area and opaque peripheral band. A median marking may be present about on site of 17/18 which is unrecognizable ventrally (A). Genital markings, lacking (B).

Internal anatomy. Gizzards, two, in v, vi (2 specimens). Intestinal origin, in xvii (2). Typhlosole, recognizable from xix, rudimentary (2). Dorsal blood vessel, single throughout (2). Last hearts, in xii (2). Sperm ducts, not traceable behind xviii, though superficial (on not within the parietes, 2).

Prostatic ducts, slender, tightly coiled close to parietes (A). Prostates, none (B). Penisetal follicles, long, perhaps as long as prostatic ducts, each in crescentic curve, common muscle strand from each pair of follicles in xvii with parietal insertion well beyond *D* and at or behind 18/19. Penial setae, long, slender, most of shaft rather crescent-shaped but shortly recurved in opposite direction ectally. Terminal ectal portion, soft, folded on itself, tip slightly wider but of nondescript shape (no reserves found, A). Ventral follicles of xx, conspicuously projecting into the coelom. The *a,b* follicles of one side of xx each contained a single seta much like those of prostatic individuals but associated with one follicle was a normally sigmoid shaft. Ventral setae of same side of xix, sigmoid. Ventral follicles of same side of xviii protrude into coelom but not as far as in xx and each contains only a sigmoid seta (B).

Spermathecal diverticulum, rather sausageshaped, with very short and slender stalk from its middle to duct entally. The coagulum within each diverticulum is constricted into lobes by ridges of variable height, discrete seminal chambers not recognized. Ventral follicles of vii-ix, enlarged, more protuberant into coelomic cavities than in adjacent segments. Copulatory setae may be present but only nondescript fragments of shafts were obtained (A). Spermathecal diverticulum, sausage-shaped, ventrally directed on lateral face of duct but not reaching

parietes, opening through single aperture (seemingly without stalk) into very ental end of spermathecal duct. Diverticular wall, thick, with numerous circular ridges (B).

Ovaries, fanshaped and with several egg strings.

Reproduction. Spermatozoal iridescence, recognizable on male funnels and in spermathecal diverticula. Reproduction is assumed to be biparental because sperm had been matured, copulation had taken place, and also because of lack of any evidence of structural degradation so often associated with male sterility (A).

Clitellum, probably at maximal tumescence. Spermatozoal iridescence, lacking on male funnels and in spermathecal diverticula. Seminal vesicles, acinous, perhaps of medium size, certainly not rudimentary. Gonads of x, xi fanshaped. One looks quite definitely like a young ovary and occasional cells in digitiform lobes do look like immature ova. Specimen (B) appears to be male sterile.

Discussion. Sterility, in earthworms, is of two sorts: fortuitous and hereditary. The first, arising as a result of some unusual interference with normal development, is male and/or female, usually in association with metameric abnormality and/or homoeosis. Rarity, in the pertinent population, and absence of exact repetition of the associated morphology proves the fortuitousness. If sterility is male only, copulation with a normally hermaphroditic earthworm can result in reproduction by the abnormal individual whereas its normal copulatory partner will be unable to reproduce itself, at least until after copulation with a normal worm. Hereditary sterility is always male, much more common and is not usually (but can be) associated with abnormal metamerism or regional homoeosis. The exactness with which the associated anatomy is repeated again and again proves this kind of sterility to be hereditary.

Hereditary male sterility requires reproduction to be parthenogenetic, though some earthworms of various families can reproduce amictically even when apparently normal spermatogenesis is profuse. In species after species, parthenogenesis has enabled gross modifications in anatomy, such as increase in number of organs, deletion of parts of organs, of whole organs or even entire sets of organs.

Hereditarily repetitive genital anatomy that departs from generic or family norms now requires consideration of the possibility that it is due to parthenogenesis. Too many megadrile species have been based on single types with defective genitalia.

The aprostatic Illinois specimen at first was thought to be a result of interference with normal embryonic development, primarily because hereditary sterility and associated conditions were unknown in the family to which *Diplocardia* belongs. The description of *egglestoni* showed that absence of prostate glands occurred commonly, perhaps in a large population, and so was hereditary. Information as to method of reproduction is lacking for *egglestoni* but there are no contra-indications to male sterility which is evidenced directly by the spermathecae, by

the size and condition of seminal vesicles, as well as indirectly by the organ deletions. Assuming reproduction to be parthenogenetic, the next question is, from which of the presently known species of *Diplocardia* could the Michigan population have been derived by any of the structural degradations so often associated with hereditary male sterility and parthenogenesis?

Prostates, more than any other structure, unless it be spermathecae, are the organs most commonly deleted. The types of *egglesoni*, except for the male terminalia, do not differ significantly from normal, amphimictic specimens of *D. singularis*. Accordingly *egglesoni* falls into the synonymy of *singularis*. The International Code of Zoological Nomenclature does not allow latinized names for clones, morphs, or infrasubspecific taxa. The Michigan population can, if necessary, be referred to as an aprostatic *singularis* morph, or, if further study shows additional differences, as Michigan morphs. Although prostates had been deleted in that population seminal grooves, now of no use, are retained although incompletely. (At full development, grooves extend at least to equators of xviii and xx.) Seminal grooves have disappeared in an Illinois morph, unless a last vestige is represented in the equatorial annulus of xix. Penial setae, though now without function, are present in the Michigan population. Those setae, in the Illinois morph, are being lost. Form of setal shafts secreted by ventral follicles of prostatic pore segments gradually changes during amphimictic adolescence and maturity. Eventually the sigmoid shape is lost and penial setae have markedly different shapes, sizes, and may be variously ornamented or sculptured. Ability to make those changes is being lost by worms of the Illinois morph. With completion of that evolutionary process, condition of the ventral setae in prostatic segments will have reverted, in adults, to a long lost ancestral condition. Ventral setae of the male pore segment are dehiscent without replacement during amphimictic adolescence or are retained in juvenile size within the body wall throughout maturity. Ability to do that is disappearing in the Illinois morph, and when it has been lost by all eight ventral follicles, setae of the former male pore segment will have reverted to a long lost ancestral condition. Especial attention is asked for those two instances as some individuals emphatically denied (*in litt.*) that reversion is possible.

The anatomical degradation, often associated with parthenogenesis, obviously has evolved further in Illinois than in Michigan morphs, at least insofar as the male terminalia are concerned. Evolution of *singularis* polymorphism seems unlikely to have been limited to two aprostatic morphs. They can be readily recognized externally because of the lack of appropriate pores at the equators of xviii and xx. Testes of Smith's aprostatic individual were not examined microscopically. Supposed ova could have been parasitic bodies, or feminization of testes may have been incomplete. Complete feminization seems likely to be

found in the unknown original home of the Illinois morph, providing reproduction has been parthenogenetic long enough. The basis for this prediction is complete conversion, in species of other families, of testes into ovaries of a quite characteristic and obviously different shape from that of male gonads. Less interesting, perhaps because of frequency elsewhere, would be reduction in number of spermathecae or deletion of the entire battery.

Parthenogenesis, in association with male sterility, has been reported hitherto from several genera (*cf.* Gates, 1956, 1960, 1961) in each of four families, Glossoscolecidae, Lumbricidae, Megascolecidae, Ocnodrilidae. The present record is the first for *Diplocardia* and also for its family, Acanthodrilidae.

A recent publication (Gates, 1960) provided information (but without discussion) as to frequency of parthenogenesis in the earthworm fauna of America north of Mexico except for a small region extending from northern California into Washington. Endemic species, according to that contribution (Table 1, p. 76) are in four genera. For *Bimastos* Moore, 1893, seven species were named. The validity of most of these remains to be established. Six according to the "New Systematics" certainly are not species at all. The needed revision now seems likely to decrease, rather than increase the number of its species. For *Eisenia*, two species were listed and further autochthones are not now expected. So little was known at that time about the genus *Diplocardia* that species were not listed. Merely to provide a definite figure for discussion, 15 of those species that had been named in the past were assumed to be valid. In *Sparganophilus*, Benham, 1892, one American species only has been recognized by recent writers.

The endemic fauna of a very large portion of North America, as known today, comprises 25 or more species in four genera. Island Ceylon, with an area of 25,332 sq. miles, has more than 70 species mostly endemic. The number of genera is 13 but will probably be increased when revisions are made. Burma (261,789 sq. miles) on the Asiatic mainland, along with adjacent and neighboring islands, has at least 150 species most of which are endemic. Why then does such a great area as the above-limited major portion of North America have so few species (60+)? One obvious answer might be that the small numbers just cited are fictitious because of our vast ignorance of American megadriles. Two genera are indeed likely to be added when properly preserved material has been made available to qualified specialists. One of these two genera now seems likely to be exotic, the other may be indigenous. Even when both are defined the number will be small with reference to size of the area being discussed. As fortuitous accumulation of occasional small samples or single individuals is replaced by systematic searches and intensive local surveys, further species perhaps should be expected. A Pakistani Visiting Professor (Bhatti, 1966), secured just in the vicinity of Philadelphia in six months,

23 species. Number of species listed for other states were: Illinois 24 (Smith, 1928), central Maine 22 (Gates, 1961), Michigan 18 (Murchie, 1956), Ohio 17 (+ 1 or 2? Olson, 1928), New York 16 (Olson, 1940), Washington 11 (Altman, 1936). Although 14 of Bhatti's species had not been reported previously from Pennsylvania, none were new and 19 are exotic on this continent. Unless much different results can be obtained in also unglaciated states further south, few new species will be added to a short continental list.

Associated with the problem posed by the paucity of continental endemics is another, that of the percentage of parthenogenesis. Six of the seven species of *Bimastos* probably are parthenogenetic. In the seventh that mode of reproduction may be optional. Parthenogenesis now is recorded for one species of *Diplocardia*. How widespread that phenomenon may be among the largest group of endemic species on this continent cannot be said. Prior to the "New Systematics," method of reproduction was unimportant and megadriles of course were always thought to be hermaphroditic and obligatorily amphimictic. Even today very few of the descriptions of earthworm species that are published provide any indication as to manner of reproduction. Six species of *Bimastos*, 1 of *Diplocardia*, and possibly at least one other, means 28 percent (or more) parthenogenesis among continental endemics.

The questions thus posed seemingly can be answered very briefly. During the Quaternary, earthworms were exterminated everywhere that glacial ice was thousands of feet thick. Implicit in recent discussion of megadrile distribution (*cf.* Omodeo, 1963) was an assumption that European species alone survived on nunataks in Greenland and Iceland, as well as on the continent itself. Until someone can show how worms could have maintained themselves during exposure to arctic conditions on denuded mountains through many millenia, the nunatak thesis needs no further consideration. Even after recession of the ice sheet was well under way, conditions for some time remained unfavorable for earthworms. Gravel, sand and clay now are often uninhabited by megadriles. Even today, at least several thousand years after the glacial epoch, earthworms are unknown in most of Alaska and northern Canada. Climatic conditions below the southernmost advance of the ice must have been far from favorable. In some such area the struggle for existence conceivably could have been so difficult that survival became possible only through adoption of parthenogenesis. If so, that area and to the north may have been the chief home of *Bimastos*. *Eisenia* (American section only) could have had a more southern distribution so that two of its species were able to survive there without being forced into parthenogenesis. *Diplocardia*, on the contrary may have only just begun to penetrate into a belt of climatically enforced parthenogenesis.

Somewhere in that belt, when it has been determined, may be found the original home of the *singularis* aprostatic morphs. No evidence has yet been presented to show that *D. singularis* reached glaciated regions

of Illinois and Michigan by its own unaided efforts. Transportation, presumably by man, probably was responsible for introduction to those area.

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